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Contributions to the embryology of the Ranunculaceæ.[1]

WITH PLATES XVII–XX.

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Various representatives of the Ranunculaceæ have been subjected to much careful study from the standpoints of morphology, histology and embryology. The well known resemblance to the monocotyledons in the structure of the vascular bundle, secondary growth of the stem and the large size of their meristematic cells, has brought to several species of this family much of that careful investigation that is usually centered upon transitional characteristics. Of all the dicotyledons certain species of the Ranunculaceæ resemble more closely the monocotyledons in the large size of their embryonic cells.[2] For this reason certain species are especially favorable for embryological studies. From a desire to know more about the development of the embryo-sac, a study of one or more species of several available genera was begun.

Prantl[3] arranges the genera of this family under three subdivisions, Paeonieæ, Helleboreæ and Anemoneæ. Of the Paeonieæ no representative was available for study; of the Helleboreæ the following species were investigated: *Delphinium tricorne* Michx., *Caltha palustris* L., *Aquilegia Canadensis* L.; of the Anemoneæ, *Ranunculus abortivus* L., *R. recurvatus* Poir., *R. septentrionalis* Poir., *Anemonella thalictroides* Spach, *Thalictrum dioicum* L. and *Hepatica acutiloba* DC.

The subject naturally embraces three phases, namely; the development of the embryo-sac, the process of fertilization, and the development of the embryo.

The following pages will be confined almost exclusively to

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[1]Contributions from the Botanical Laboratory of the University of Indiana.
[2]Strasburger, Histologische Beiträge 5: 118. 1893.
[3]Natürlichen Pflanzenfamilien.

the development of the embryo-sac and its behavior previous to fertilization. The different species will be taken up in the order indicated above.

Delphinium tricorne.—As is well known the ovules of Delphinium arise as nipple-like protuberances from the infolded margins of the carpophyll. The epidermal and hypodermal rows of cells of the carpophyll pass uninterruptedly over this rudiment of the ovule. At the apex of the protuberance may be seen one or frequently more hypodermal cells distinguishable by their larger size (fig. 2). The cell which ultimately gives rise to an embryo-sac will, for greater clearness, be spoken of in this paper as the initial cell of the embryo-sac, while the term mother-cell will be reserved for the lower one of the longitudinal row of cells arising from subsequent divisions of this cell. In the very young rudiment of the ovule (fig. 1) in a large number of cases the initial cell of the embryo-sac is not perceptibly different from the other hypodermal cells nor the cells of the young ovule in general. It is usually stated that the initial cell of the embryo-sac is the terminal one of an axial row of cells of the nucellus, especially in monocotyledons which possess small ovules. In larger, small-celled ovules, those of the dicotyledons particularly, proof of an axial row is indeed difficult, if not quite impossible. In few cases in Delphinium an axial row could be determined (fig. 2); but it is very evident, even in the most favorable cases, that the initial cell or cells sustain a closer genetic relationship with the hypodermal layer than with any other cells of the nucellus (figs. 1–3).

The initial cell now increases in size, and divides by a transverse wall into two cells, the lower being frequently a little larger than the upper (figs. 4, 5, 7). When the first division is completed in the initial cell, the epidermal cells of the nucellus have divided by periclinal walls, and the inner integument has attained a level with the apex of the nucellus. Each of the two resulting cells (fig. 5) now divide by a wall parallel to the first, thus giving rise to four cells by two successive divisions of the initial cell of the embryo-sac. These transverse walls are very thin membranes without being the least swollen in the instances figured. As far as observation extended, the division of the lower cell preceded that of the upper, as will be seen in figs. 6 and 7. These divisions follow as a rule in rapid succession. The lower one of the

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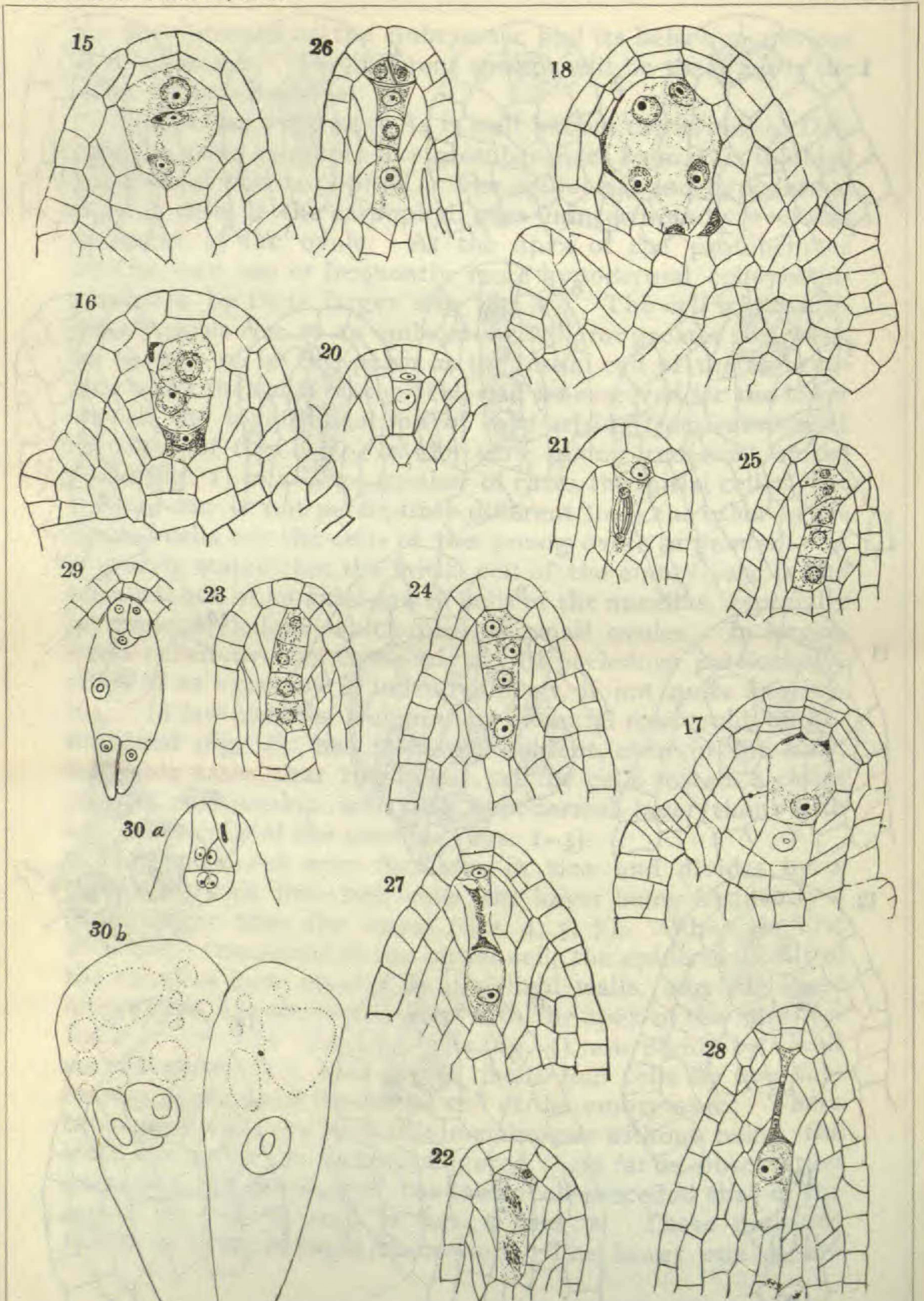

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row of four cells now becomes a mother-cell of the embryo-sac. It increases in size, gradually absorbing the three cells above and also the adjacent cells of the nucellus, a process that almost invariably obtains in all angiosperms. In fig. 8 the mother-cell may be seen separated from the disorganized remains of the three superposed cells by an arched wall which is somewhat swollen.

The nucellus here has elongated, so that at this stage of development the three disorganized cells do not appear as flattened caps above the encroaching mother-cell, but seem to form only a narrow cavity containing a structureless substance which stains deeply. I have not been able to show this accurately in the pen drawing. This cavity is made narrow both by the increase in length of the nucellus and by the turgor of the cells immediately surrounding it. The walls of the turgid cells here in question, which border upon the cavity, are usually much swollen. The mother-cell now develops into the embryo-sac in the normal manner. The mature embryo-sac is covered by the nucellar cap varying from two to four cells in thickness. The antipodal cells attain an extraordinary size compared with that of the egg-apparatus, as a glance at figs. 10*a* and 10*b* will plainly show. This condition of affairs exists in the embryo-sac at the time of anthesis or shortly before. The three cells almost always lie side by side in the same horizontal plane, consequently only two are shown in the figure, the other being in the next successive section. They gradually increase in volume with the subsequent growth of the embryo-sac, and persist for a time after fertilization, when they are finally absorbed. About the time of fertilization they may be seen upon a projection of the chalaza at that end of the sac which has now become very broad. However, the position of the antipodal cells varies considerably in different ovules. Strasburger has called attention to the enormous size of the antipodal cells in *Delphinium villosum.*[4] In Delphinium tricorne the writer did not find the difference to be quite so great. We shall return to this phenomenon further on.

The only account of the development of the embryo-sac in any representative of the Ranunculaceæ to which I have access is that given by Strasburger[5] for *Myosurus minimus.* In

[4]Strasburger, Ueber Befruchtung und Zelltheilung 38. 1878.
[5]Strasburger, Die Angiospermen und Gymnospermen 13. 1879.

this plant the author finds that the initial cell gives rise to a row of only three cells, the lower one of the series developing into the embryo-sac in the normal way. It will be seen that Delphinium differs from Myosurus in that four cells result from two successive cell divisions of the initial cell, of which the lower one gives rise directly to the embryo-sac. It is not improbable, however, that occasionally only three cells are formed here as in Myosurus, a phenomenon that was observed in other genera to be mentioned later.

The most remarkable phenomenon met with here is the presence of two and sometimes more initial cells and their development into mature embryo-sacs. In figs. 1 and 3 may be seen two initial cells of about equal size. In a number of cases one of the cells was somewhat larger than the other. The larger would in all probability take the upper hand of the smaller, thus crowding it out when only one embryo-sac would be the result. Frequently two cells were observed in later stages of development (fig. 7), both of which would, without doubt, produce mature embryo-sacs. As a rule one cell is a little in advance of its neighbor in development (fig. 7, the cell on the left). This state of things is not exceptional, but in some carpels a large number of ovules presented two, and occasionally three, initial cells. It is certain that every initial cell does not ultimately result in a mature embryo-sac, for it seems that there is unquestionably a "struggle of the parts" here as elsewhere. No more than two embryo-sacs were observed in one ovule. In fig. 9 are shown two fully developed embryo-sacs, apparently of equal size and importance. The antipodal cells lie side by side in a plane at right angles to the plane of the section. By focusing deeper other nuclei could be seen, and in an adjacent section the other antipodal cells were visible. The two embryo-sacs were contiguous for their whole length, separated only by a very thin and indistinct membrane. For lack of time a very large number of ovules was not examined to ascertain the frequency of the phenomenon, nor is it known to the writer whether more than one embryo-sac is fertilized, and in that event whether more than one embryo ever reaches maturity in a single seed of Delphinium.

We do not have to do here with an isolated phenomenon, for the presence of more than one embryo-sac in one ovule has been observed several years ago by Hofmeister,[6] Tulasne, Schacht and others.

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[6]Strasburger, Ueber Befruchtung und Zelltheilung 36 and foot note.

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